

Seasonal study of aquatic invertebrates in five sets of latitudinally separated gnammas in southern Western Australia

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Gnammas (i.e. rock pools) are characteristic habitats on granitic inselbergs in southern Western Australia and, though their basic limnology is known, much remains to be learnt on the distribution patterns and seasonality of their fauna. In this study 10 pools on five inselbergs (Mt Madden, Hyden Rock, Yanneymooning Rock, Bullamany Rock and Walga Rock) across a 700 km latitudinal climatic gradient were studied during the flooded period from May to October 2010. Seventy-three taxa inhabited the five rocks and showed declining species richness from south to north promoted by decreasing hydroperiod and reliability to the north. Passively dispersing crustaceans dominated with 47% of taxa, and almost all of the most abundant species, while 41% of taxa were seasonal colonising insects. Many pools had 25–30 invertebrate species each, far more than rock pools elsewhere in Australia and overseas. Most of the dominant species were widespread, more localised taxa included cyclopoids and the snail *Glyptophysa* sp. in the south and the notostracan *Triops* n. sp. in the north. Regional endemism and specialisation to live in gnammas was high as a consequence of past climatic changes linked with the role of these pools as refuges. Most of the dominant species were filter feeders on algae and allochthonous and autochthonous organic matter and the dominant predators were planarians and beetle larvae. Most species peaked in abundance in August and September, with large branchiopods (mainly the anostracan *Branchinella longirostris*) peaking before cladocerans and with ostracods last. Active dispersers included hemipterans, coleopterans and dipterans; almost all were widespread opportunists, but at least one *Paroster* beetle species was a gnamma specialist. Chironomids were dominated by gnamma specialists *Paraborniola tonneri* and *Allotrisocladius* sp 1 which survive the dry summer *in situ* as cryptobiotic 4th instars and emerge soon after the ponds first fill, and by the temporary pond specialist *Chironomus tepperi* which invaded from elsewhere when the ponds fill. Stones in the gnammas were important for at least two species: *Triops* n.sp uses them to hide from predators and the snail *Glyptophysa* aestivates underneath them. Succession in these pools was best explained by the tolerance model in which each taxon developed at its own pace, largely unaffected by other taxa.

KEYWORDS: beetles, *Boeckella opaquia*, branchiopods, chironomids, cladocerans, latitudinal gradient, nematodes, ostracods, *Paroster*, planarians, rock pools, seasonal succession

INTRODUCTION

A number of surveys of pools on granite outcrops in southwestern Western Australia have revealed a diverse aquatic fauna with many endemic species and rock pool specialists (Jones 1971; Bayly 1982 1997; Pinder et al. 2000, Timms 2006; Jocqué et al. 2007a). Prominent amongst the crustaceans are branchiopods *Branchinella longirostris* and *Limnadia badia*, the copepod *Boeckella opaquia*, cladocerans *Daphnia jollyi*, *Macrothrix hardingi*, *Plurispina* spp., *Celsinotum* spp., and ostracods *Bennelongia* sp563, *Cypretta* spp, *Ilyodromus* spp., *Cypricercus* spp (all *sensu* Pinder et al. 2000). The most common insects are chironomids like *Allotrisocladius* spp and *Paraborniola tonnoiri* (Edward 1968) and some new species of *Paroster* beetles (Hendrich & Frey 2008). Distribution of taxa across the Wheatbelt and Goldfields is heterogeneous, especially for large branchiopods (Timms 2006) and unpublished studies (Jocqué 2007; B. Vanschoenwinkel et al. pers.comm. 2011) suggest a decline in overall species richness and change in community structure from south to north.

The Western Australian gnammas have been poorly characterised in terms of geomorphology, hydrology and successional patterns, but are broadly categorised into pan gnammas, pit gnammas and pipe (or cylindrical) gnammas (Twidale & Corbin 1963; Bayly et al. 2011; B V Timms unpubl. data). Most studies dealt almost exclusively with pan gnammas avoiding variation associated with distinctive but less speciose and different communities of pit and pipe gnammas (Bayly et al. 2011; B V Timms unpubl. data). Little is known about successional changes and regional variation in southwest Western Australia. Temporally constrained studies performed in early, mid or late successional stages or in localised areas could give unrepresentative results. Concerning the latter, Bayly's (1982) study of pools at Northcliffe, far to the south of the main Wheatbelt presented a reduced fauna than typical for Wheatbelt pools and the lack of some common dominants such as *Limnadia badia*, *Daphnia jollyi* and *Macrothrix hardingi*, while the large branchiopod *Caenestheriella mariae* seems to be mainly in gnammas fringing the northern and eastern wheatbelt (Timms 2006).

This study examines the association of successional stage on species richness and community composition of invertebrates in pan gnammas. Particular attention will

be paid to when pool communities are the most speciose and whether or not there are major changes in community structure between early, mid and late stages of the pools' hydroperiod. In addition, pools were chosen on a long north-south gradient, in order to investigate the effect of climate on invertebrate distribution and population size in the pools.

METHODS

Five granite outcrops, Mt Madden ($33^{\circ}14'22.6''\text{S}$, $119^{\circ}50'33.6''\text{E}$), Hyden (=Wave) Rock ($32^{\circ}26'43.6''\text{S}$, $118^{\circ}54'14.4''\text{E}$), Yanneymooring Rock ($30^{\circ}42'50.5''\text{S}$, $118^{\circ}33'19.2''\text{E}$), Bullamany Rock ($29^{\circ}09'50.9''\text{S}$, $117^{\circ}39'40.4''\text{E}$) and Walga Rock ($27^{\circ}24'14.2''\text{S}$,

$117^{\circ}27'48.8''\text{E}$), were chosen roughly equidistantly along a north-northwest-south-southeast line ~700 km long (Figure 1). Ten pan gnammas on each rock ranging over various sizes from ~1 m diameter and ~8–12 cm deep to the largest available (often ~5 m diameter and 20–40 cm deep) were studied. A range of pool sizes was chosen to: (i) represent the variety found in nature; and (ii) cover the possibility of species richness being influenced by pool size (Bayly 1997). Most of the pools selected were within 100 m of each other near the summit of each rock, but some outliers were located downslope, thus extending the maximum distance between pools to ~250 m on Mt Madden, Yanneymooring and Bullamany Rocks, and to ~150 m on Hyden Rock and Walga Rock. Sampling commenced on 24 May 2010, then at three-weekly intervals until early October and took 3–4 days

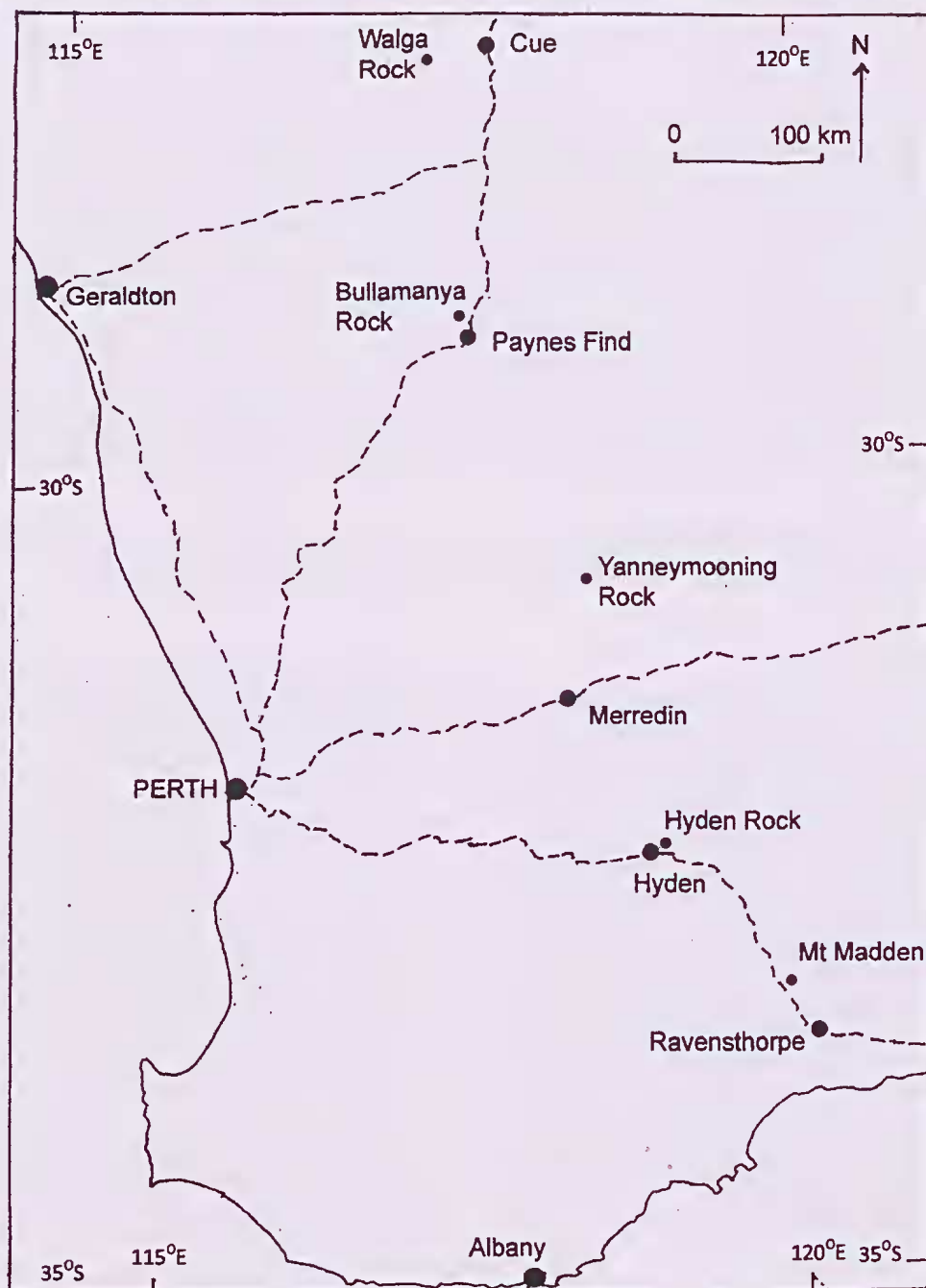


Figure 1. Map of southwestern Western Australia showing the location of the five rocks with reference to nearby locations.

each trip and was always conducted south to north. Overall the field work took 19 weeks and each rock was visited seven times almost synchronously (maximum 3–4 days apart). More frequent sampling would have been desirable, but sampling damages the pools physically and also conceptually could result in overharvesting (see below) from limited populations, but if this happened it was not noticed.

At each pool, water depth was determined with a stiff tape measure at the deepest point to the nearest 0.5 cm. Conductivity was measured with a Hanna HI8733 meter. There was no point in measuring water clarity as the pools were almost always crystal clear, nor water temperature as it varied widely diurnally. However, some seasonal highs and lows were noted, using an alcohol-in-glass thermometer accurate to $\pm 0.5^\circ\text{C}$.

Two different nets were used to sample the fauna. A small plankton net, aperture 15×10 cm, 30 cm long and of mesh $159 \mu\text{m}$, was used to sample microfauna in the water column and on the bottom surface (the latter by disturbing the sediment and then passing the net through the slurry). A household sieve, 20 cm in diameter and of mesh size ~ 2 mm was used for larger invertebrates. The number (5–20) of sweeps of each device was adjusted to pool size so that about 50% of the water volume in small pools was sampled down to 5% in the very large pools. This introduced an error between pools in estimating abundance and species richness, but the bias was constant between rocks and sampling dates. To have studied one pool size, if 10 pools per rock and 50 pools overall were exactly possible, would have introduced a greater misrepresentation in overall species richness per rock, given the variability between pools of different size (Vanschoenwinkel *et al.* 2009).

Plankton were concentrated by settling first in dilute ethanol, then pouring off supernatant and preserving in $>70\%$ ethanol. Sieve collections were handpicked in the field from a sorting tray; one individual (a few of more abundant chironomids) of each species was kept and preserved in 70% ethanol and the remainder returned alive to the pond. This protocol was adopted as there are many microinvertebrates with short life cycles in the pools so the loss of a few hundred every three weeks was thought to be insignificant, but to remove most of the few macroinvertebrates individuals on each sampling occasion would have considerably depleted populations. The numbers of sweeps to get representative samples were chosen based on a preliminary study the previous year. Even so, no matter how intense the sampling, and indeed the sampling of just 10 pools per rock, not all species present per pool/rock were necessarily caught (Jocqué *et al.* 2007a). Furthermore, though replicate sampling is desirable, it was not possible in smaller pools (due to unacceptable environmental damage and the sampling of a decreasing population) and was not employed in order to maintain a reasonably similar sampling regime across the pool spectrum. Sampling protocol was a compromise between damage to the pool, idealistic catching of all the fauna, and practical considerations of efficient time per unit effort.

In the laboratory each plankton collection for each pool was examined completely under an Olympus SZ61 stereomicroscope, species identified and the number of each species estimated on a log scale. The number of

macroinvertebrates caught in the sieve was also estimated on a log scale. In a detailed study (B V Timms unpubl. data) of 96 pools on Anderson Rock (40 km north of Hyden Rock) distribution of invertebrates over the whole rock was heterogeneous and it depended on which 10 pools were sampled as to the perception of species richness and abundance for that rock outcrop. This problem is unsolvable unless all pools are sampled – species accumulation curves at Wave Rock continued rising even after 50 pools were sampled, albeit slowly after 10 pools (Jocqué *et al.* 2007a) but by sampling the same 10 pools each time on each rock, any bias was constant over the season.

Daily rainfall during 2010 was obtained from the Bureau of Meteorology website for weather stations as close as possible for each rock: for Mt Madden from Mt Madden 1.4 km southeast, for Hyden Rock from Hyden 3 km east, for Yanneymooning from Wattoning 34 km west, for Bullamany Rock from Paynes Find 11 km south, and for Walga Rock from Cue 43 km east. Data are presented as monthly totals in Figure 2.

Relationships between assemblages on the five rocks were investigated using PRIMER (v5) (Clarke & Gorley 2001). Average seasonal abundance data of invertebrates from the mid-July, early and late August and mid-September trips (Table 1) was log (N+1) transformed prior to multivariate analysis. Non-metric multidimensional scaling, based on Bray–Curtis similarity index was used to represent assemblage composition in two-dimensional space. Relative distance apart in the ordination represents relative dissimilarity.

RESULTS

Pools

Unfortunately, 2010 was a drought year, so pools did not fill to their full capacity, nor for as long a period as usual. For the period April to October, Mt Madden rainfall was 56% of average, Hyden Rock 43%, Yanneymooning 25%, Bullamany Rock 69% and Walga Rock 57% (Figure 2). Pools on Mt Madden (the southernmost rock) held water continuously from May to September but by early October most were dry (Figure 3). On Hyden Rock, pools were never as full and they started drying earlier, so that almost all were dry by early October. On Yanneymooning a few pools dried in August, but filled again in September, only for all to dry by early October. By contrast at Bullamany Rock only one pool dried in August and half still had water in early October. Walga Rock's pools initially had some water, but dried completely in August and partially filled again in September to dry again by early October (Figure 3). Pools with water on the three southern rocks were of maximum number and cumulative depth in mid July, while Walga Rock's pools were maximal in mid-September. Bullamany's pools were intermediate between these two extremes (Figure 3).

During winter, the minimum water temperature measured during daylight was 3.0°C (on 22 July at Hyden Rock). The maximum water temperature observed was 26.4°C at Bullamany Rock on 6 October. While almost all pools contained crystal-clear water and hence their floors were clearly visible, occasionally a few

Table 1 Species occurrences on the five rocks

Major group	Species	Madden		Hyden		Yanney		Bullam		Walga	
		2009	2010	2009	2010	2009	2010	2009	2010	2009	2010
Turbellaria	unidentified black planarian	o	x	o	x	o	x	o	x	-	-
	unidentified green planarian	o	xxxx	o	xx	o	r	-	x	-	-
	unidentified rhabdocoel	-	r	-	r	-	-	-	-	-	-
Nematoda	unidentified nematodes	o	x	o	xx	o	r	o	-	o	x
Branchiopoda	<i>Branchinella longirostris</i>	-	x	-	r	o	xx	o	xxx	o	x
	<i>Limnadia badia</i>	o	xxx	o	x	o	xx	o	xxx	-	-
	<i>Caenestheriella mariae</i>	-	-	-	-	-	r	o	xx	o	x
	<i>Triops n. sp.</i>	-	-	-	-	-	-	-	r	o	x
	<i>Daphnia jollyi</i>	-	-	o	-	o	r	o	r	-	-
	<i>Ceriodaphnia sp.</i>	o	xxxx	o	xxx	-	-	-	-	-	-
	<i>Moina australiensis</i>	-	x	-	r	o	-	-	-	-	-
	<i>Ilyocryptus sp.</i>	o	r	-	-	-	-	-	-	-	-
	<i>Macrothrix lardingi</i>	-	r	o	-	-	xx	-	xxx	-	-
	<i>Macrothrix spp.</i>	o	xxx	o	x	-	r	-	x	-	-
	<i>Neothrix spp.</i>	o	r	o	x	o	x	-	xx	-	-
	<i>Alona macrocopa</i>	o	r	-	r	-	r	-	-	-	-
	<i>Alona rigidicaudis</i>	o	r	o	-	-	-	-	-	o	-
	<i>Alona spp.</i>	-	r	-	r	-	-	-	-	-	-
	<i>Chydorus hybridus</i>	o	r	-	r	-	-	o	-	-	-
	<i>Ephemeroporus tridentata</i>	o	xxx	-	x	-	r	-	x	-	-
	<i>Leberis aenigmatica</i>	-	r	o	xx	o	xx	-	r	-	-
	<i>Monospilus diporus</i>	-	-	o	r	-	-	-	-	-	-
	<i>Planirculus alticarinatus</i>	o	xxx	o	r	o	r	o	-	-	-
	<i>Plurispina multituberculata</i>	o	xxx	o	xx	o	r	-	r	-	-
	<i>Rak sp</i>	o	x	o	r	-	-	-	-	-	-
Copepoda	<i>Boeckella opaquia</i>	o	xxxx	o	xxx	o	xxx	o	xxxx	-	x
	<i>Metacyclops laurentisae</i>	o	x	-	-	-	-	-	-	-	-
	harpacticoid Sp 674 (SAP)	-	r	-	-	-	-	-	-	-	-
Ostracoda	<i>Beimelonia sp 563.</i>	o	xxx	o	x	-	r	o	x	o	r
	<i>Candonocypris spp.</i>	-	x	-	x	-	r	-	r	-	-
	<i>Cypretta baylyi</i>	-	x	o	x	o	r	o	x	-	-
	<i>Cypricercus sp 637</i>	o	xxxx	o	xxx	-	xxx	o	xxx	o	-
	<i>Cypricercus spp.</i>	-	r	-	-	-	-	-	-	-	-
	<i>Ilyodromus anaplicolis</i>	o	xxx	o	xxx	o	x	o	xx	o	R
	<i>Ilyodromus sp. 630</i>	-	r	-	r	-	r	-	-	-	-
	<i>Ilyodromus spp.</i>	-	r	-	-	-	-	-	-	-	-
	<i>Limnocytheria porphyetica</i>	o	r	o	r	o	-	o	r	-	-
Odonata	<i>Sarscypridopsis spp.</i>	o	xxx	o	xxx	o	-	o	-	-	-
	<i>Hemicordulia tau</i>	-	r	-	-	o	r	-	x	-	-
Hemiptera	<i>Micronecta sp.</i>	o	r	o	r	o	x	-	-	-	r
	<i>Agraptocorixa spp.</i>	o	r	o	r	-	r	-	-	o	r
	<i>Anisops gratus</i>	-	-	o	r	-	r	o	r	-	-
	<i>Anisops hyperion</i>	o	r	-	-	-	-	-	-	-	-
	<i>Aniops thienemanni</i>	o	r	o	r	-	r	-	-	-	-
Coleoptera	<i>Allodessus bistrigatus</i>	o	r	o	r	-	r	o	-	o	-
	<i>Antiporus gilberti</i>	o	r	o	r	-	-	-	r	-	-
	<i>Berosus sp</i>	-	-	o	r	-	-	-	r	-	r
	<i>Eretes australis</i>	-	-	-	r	-	r	-	r	-	r
	<i>Halochares sp.</i>	-	-	-	r	-	-	-	-	-	-
	<i>Hyphidrus elegans</i>	o	-	-	-	-	-	-	-	-	-
	<i>Hydrovatus sp.</i>	-	-	-	-	-	-	-	r	-	-
	<i>Limnoxenus novaezealandiae</i>	-	r	-	-	-	-	-	-	-	-
	<i>Lancetes lanceolatus</i>	-	r	-	r	-	-	-	-	-	-
	<i>Megaporus howetti</i>	-	r	-	-	-	-	-	-	-	-
	<i>Necterosoma sp.</i>	-	-	-	-	-	-	-	-	-	r
	<i>Paroster nr michaelsoni</i>	-	r	-	r	-	x	-	r	-	r
	<i>Rhantus suturalis</i>	-	-	-	r	-	-	o	r	-	-
	<i>Sternopriscus multimaculatus</i>	o	r	o	r	o	r	o	-	o	r
	unidentified curculionid	-	-	-	-	-	r	o	-	-	-
	<i>Allodessus</i> larvae	o	-	o	-	o	-	o	-	o	-
	<i>Antiporus</i> larvae	o	r	o	r	-	-	-	r	o	-
	<i>Berosus</i> larvae	-	-	-	-	-	-	-	-	o	-
	<i>Enochrus</i> larvae	o	-	-	-	-	-	-	-	-	-
	<i>Lancetes</i> larvae	-	r	-	r	-	r	-	-	-	-
	<i>Limnoxenus</i> larvae	-	-	o	-	-	-	-	-	-	-
	<i>Paroster</i> larvae	-	r	-	r	o	x	o	x	-	r
	<i>Sternopriscus</i> larvae	o	-	o	-	o	-	o	-	o	-

Table 1 (cont.)

Major group	Species	Madden		Hyden		Yanney		Bullam		Walga	
		2009	2010	2009	2010	2009	2010	2009	2010	2009	2010
Diptera	juvenile chironomids	o	x	o	r	o	x	o	x	-	-
	<i>Allotrissocladius</i> sp. L	o	r	o	r	o	x	o	x	o	-
	<i>Chironomus lepperi</i>	-	-	o	-	-	x	-	xx	-	-
	<i>Paraborniola tonnoiri</i>	o	r	o	x	o	x	o	x	o	xxx
	<i>Parakeiffieriella variagatus</i>	-	-	-	r	-	r	-	r	-	-
	<i>Procladius</i> sp.	o	r	-	x	-	x	o	x	-	-
	<i>Tanytarsus</i> sp.	-	-	-	-	-	-	-	-	-	-
	<i>Dasyhelia</i> sp.	o	r	o	x	o	r	o	x	-	x
	<i>Aedes alboannulatus</i>	-	r	-	r	-	r	-	-	-	-
	<i>Culex starkeae</i>	-	-	-	-	-	-	-	r	-	-
	stratiomyid larvae	-	-	-	r	-	-	-	-	-	-
	tabanid larvae	-	-	-	-	-	r	-	-	-	-
Arachnida	hydrocarinid mites	-	-	-	-	o	-	o	-	-	-
	trombidoid mites	-	-	-	-	-	r	-	r	-	-
	oribatid mites	o	-	o	-	-	-	-	-	-	-
Mollusca	<i>Glyptophysa</i> sp.	o	xxx	-	-	-	-	-	-	-	-
Total		37	51	36	41	25	41	26	37	16	17
Grand total (2009 + 2010)		54		47		45		45		23	
Mean MSR peak period		30.75		26.5		29.5		26.5		10.6	

Presence in 2009 noted by an 'o' and abundances in 2010 given variously by 'r' for rare up to 'xxxx' for various degrees of abundance. Abundances are averages over the four plateau samples (July to Sept). For totals of species, juveniles are only counted if no adults in that genus have been recorded.

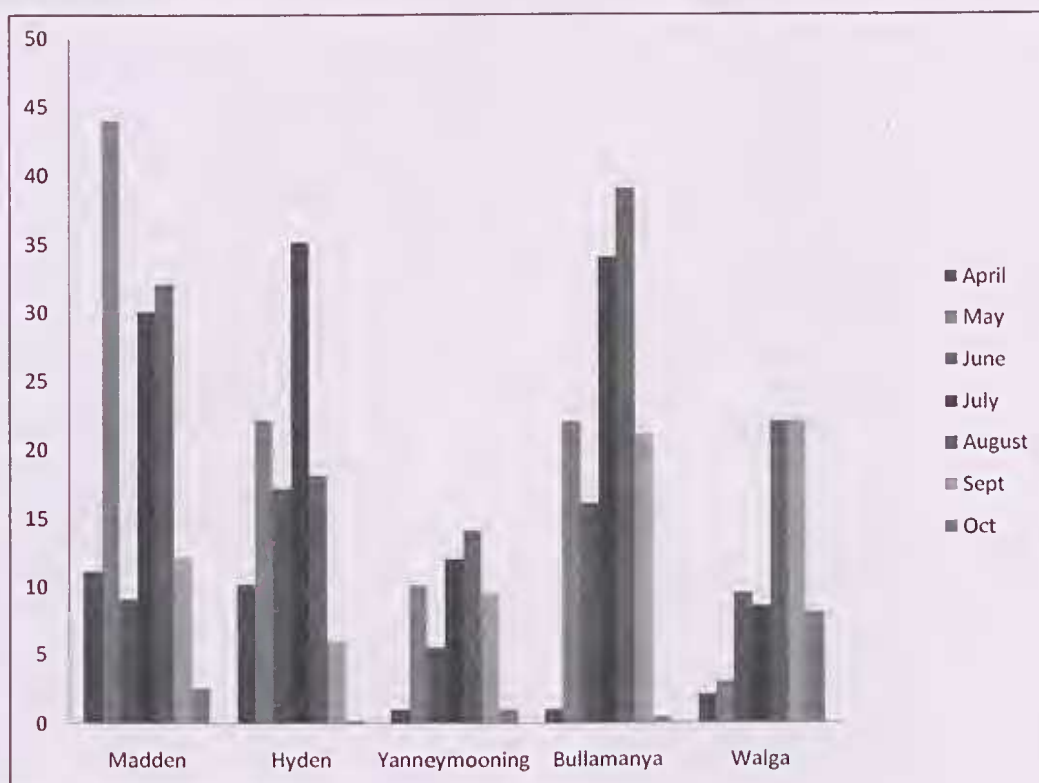


Figure 2. Monthly rainfall in millimetres at each of the five sites during 2010

pools had cloudy water with Secchi disc values less than their depths (i.e. at 10–20 cm, but still not particularly turbid) Conductivities varied between 45 and 1300 $\mu\text{S}/\text{cm}$, with values typically increasing as pools dried. Some pools contained abundant filamentous algae and most southern pools (particularly on Mt Madden and Hyden and to some degree on Yanneymooring) had a floor of aquatic plants, mainly of *Isoetes* sp. and *Glossostigma* sp.

Species richness

Seventy-two invertebrate taxa were identified in this group of gnammas (Tables 1, 2). In that some taxa represented more than one species [as indicated in the species lists (Table 1)], the total number of species present was probably about 5–10% more than this. Cumulative species richness per rock (over the entire study) decreased from south to north, with the decline steeper

Table 2 Number of pools of the 10 studied on each rock with each species

Major group	Species	Madden	Hyden	Yanney	Bullen	Walga
Turbellaria	unidentified black planarian	7	9	8	9	-
	unidentified green planarian	10	4	1	2	-
	unidentified rhabdocoel	1	1	-	-	-
Nematoda	unidentified nematodes	5	8	7	-	4
Branchiopoda	<i>Branchinella longirostris</i>	4	2	8	9	6
	<i>Limnadia badia</i>	6	8	6	10	-
	<i>Caenestheriella mariae</i>	-	-	2	5	8
	<i>Triops</i> n. sp.	-	-	-	2	4
	<i>Daphnia jollyi</i>	-	-	1	1	-
	<i>Ceriodaphnia</i> sp.	10	10	-	-	-
	<i>Moina australiensis</i>	2	2	-	-	-
	<i>Ilyocypris</i> sp.	1	-	-	-	-
	<i>Macrothrix hardingi</i>	1	-	4	6	-
	<i>Macrothrix</i> spp.	7	3	1	2	-
	<i>Neothrix</i> spp.	1	4	3	7	-
	<i>Alona macrocopa</i>	1	2	1	-	-
	<i>Alona rigidicaudis</i>	1	-	-	-	-
	<i>Alona</i> spp.	2	1	-	-	-
	<i>Chydorus hybridus</i>	1	1	-	-	-
	<i>Ephemeroporus tridentata</i>	5	2	1	4	-
	<i>Leberis aenigmatica</i>	3	6	4	2	-
	<i>Monospius diporus</i>	-	1	-	-	-
	<i>Planicirculus alticarinatus</i>	8	3	2	-	-
	<i>Plurispina multituberculata</i>	7	7	2	2	-
	<i>Rak</i> sp.	3	1	-	-	-
Copepoda	<i>Boeckella opaquia</i>	10	10	10	10	8
	<i>Metacyclops laurentiisae</i>	4	-	-	-	-
Ostracoda	harpacticoid Sp 674 (SAP)	1	-	-	-	-
	<i>Benueolongia</i> sp 563.	9	5	2	5	4
	<i>Candonocypris</i> spp.	4	5	3	5	-
	<i>Cypretta baylyi</i>	3	4	1	4	-
	<i>Cypricercus</i> sp 637	9	10	9	10	-
	<i>Cypricercus</i> spp.	1	-	-	-	-
	<i>Ilyodromus anaplicolis</i>	8	9	5	9	3
	<i>Ilyodromus</i> sp. 630	1	1	1	-	-
	<i>Ilyodromus</i> spp.	1	-	-	-	-
	<i>Limnocytheria porphyetica</i>	2	2	-	1	-
	<i>Sarscypridopsis</i> spp..	7	8	-	-	-
	<i>Hemicordulia tau</i>	2	-	2	3	-
Odonata	<i>Micronecta</i> sp.	4	5	5	-	2
Hemiptera	<i>Agraptocorixa</i> spp.	3	3	2	-	1
	<i>Anisops gratus</i>	-	2	3	3	-
	<i>Anisops hyperion</i>	2	-	-	-	-
Coleoptera	<i>Anisops thienemanni</i>	5	5	4	-	-
	<i>Allodessus bistrigatus</i>	7	3	3	-	-
	<i>Antiporus gilberti</i>	2	3	-	2	-
	<i>Berosus</i> sp.	-	2	-	2	3
	<i>Eretes australis</i>	-	2	3	3	2
	<i>Halochares</i> sp.	-	2	-	-	-
	<i>Hydrovatus</i> sp.	-	-	-	2	-
	<i>Limnoxenus novaezealandiae</i>	2	-	-	-	-
	<i>Lancetes lanceolatus</i>	1	1	-	-	-
	<i>Megaporus howetti</i>	2	-	-	-	-
	<i>Necterosoma</i> sp.	-	-	-	-	1
	<i>Paroster</i> nr <i>michaelseni</i>	4	5	7	5	2
	<i>Rhantus suturalis</i>	-	2	-	1	-
	<i>Sternopriscus multimaculatus</i>	5	4	3	-	2
	unidentified curculionid	-	-	1	-	-
	<i>Antiporus</i> larvae	3	2	-	1	-
	<i>Laucetes</i> larvae	1	1	1	-	-
	<i>Paroster</i> larvae	4	4	7	5	2
	<i>Sternopriscus</i> larvae	-	-	-	-	-
Diptera	juvenile chironomids	7	6	8	5	-
	<i>Allotrissocladius</i> sp. L	4	2	6	5	-
	<i>Chironomus tepperi</i>	-	-	5	5	-
	<i>Parabornia tonuoiri</i>	2	6	6	7	9
	<i>Procladius</i> sp.	2	3	4	3	-
	<i>Dasyhelius</i> sp.	4	6	3	5	5
	<i>Aedes alboannulatus</i>	1	3	1	-	-
	<i>Culex starkeae</i>	-	-	-	1	-
Arachnida	trombidoid mites	-	-	3	2	-

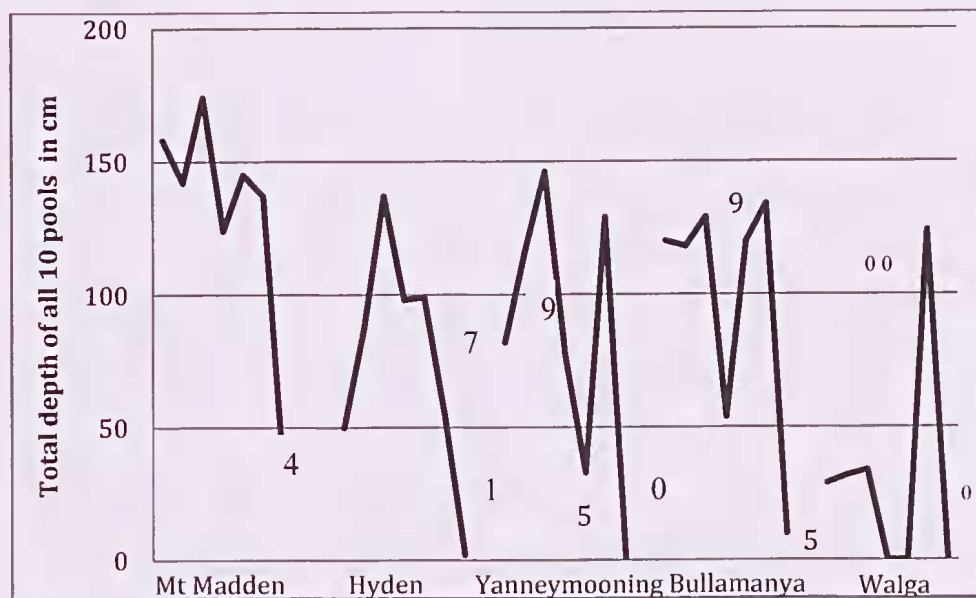


Figure 3. Total depth of all 10 pools on the five rocks over the seven samplings (May to October). Number of pools holding water was usually 10 per rock, except where indicated.

towards the north: Mt Madden had 51 taxa, Hyden 41, Yanneymooring 41, Bullamany 37 and Walga 17. Species richness was greater in 2010 than in the preliminary 2009 survey because the more thorough sampling in 2010 netted many uncommon species (Tables 1, 2). Species richness for each set of 10 pools varied between trips and was usually minimal in early and late trips, peaking for the middle trips. Early visits missed late hatching and late colonising species whereas late visits lost quicker drying pools and their fauna. Mean momentary species richness per rock hardly decreased south to north except for Walga Rock, and plateaued in July to September (from 9–18 weeks after filling): Mt Madden 30.75 ± 0.96 species, Walga 26.5 ± 4.1 , Yanneymooring 29.5 ± 3.0 , Bullamany 26.5 ± 4.4 , Walga 10.6 ± 2.1 . Mt Madden's plateau continued longer and species richness hardly varied in keeping with its pools being more stable hydrologically (Appendix 1).

Differences between southern and northern sites were characterised by a decrease in certain taxa in the two northern sites, notably the absence and reduced presence of cladocerans at Walga and Bullamany, respectively, compared to up to 15 species at southern sites. Walga was also characterised by the absence of planarians and fewer ostracods, hemipterans and beetles. On the other hand, Mt Madden had some taxa not seen on other rocks, notably a cyclopoid and harpacticoid copepod, a snail and extra insects. Counter to this pattern was the presence of two large branchiopods (*Caenestheriella mariae* and *Triops* n. sp.) only at the northern rocks and of *Daphnia jollyi* and hydrocarinid and trombidoid mites at Yanneymooring and Bullamany. In the latter two rocks *Macrothrix hardingi* replaced *Ceriodaphnia* n. sp. as the most common cladoceran. However all sites, except Walga, shared most of the species encountered.

Relative dominance of the most abundant species (Figures 4–9) showed *Boeckella opaquia* to be the most abundant species on average at four of the five sites and present at the fifth. The next most widespread and abundant species was *Cypricercus* sp. 637, followed by a

large group abundant on a few rocks, but not present on all. These include *Ceriodaphnia* sp. and green planarians (southern rocks), *Branchinella longirostris*, *Limnadia badia*, *Neothrix armata* and black planarian (middle rocks) and *Parabornella tounoiri* and *Caenestheriella mariae* (northern rocks). An alternative view of relative dominance is gained by analysing the number of pools on each rock containing each species (Table 2). Overall this confirmed the common and rare species, but in general uncommon insects occurred in more pools than uncommon crustaceans. The ordination diagram from a multivariate analysis (Figure 10) showed a relationship best explained by factors associated with latitude, though the separation between Yanneymooring and Bullamany was slight. Mt Madden in the far south and Walga Rock in the far north were the most variant, probably due to the dominance of some extra species at Mt Madden and the restricted species richness at Walga Rock.

Phenology

There was little sequential appearance of species during the aquatic stage of the gnammas; most species peaked according to their speed of development (Figures 4–9, Appendix 1). Southern pools had a earlier start in broad agreement with filling associated with rainfall—Mt Madden with 11 mm in April was the most advanced when sampled commenced in late May, and Bullamany the least advanced with only 0.8 mm in April. Differences in speed of community development soon faded on subsequent sampling trips, except at Walga which exhibited a stop-start pattern associated with its erratic hyperperiods.

Branchiopod larvae and chironomids (mainly *Parabornella tounoiri*) appeared first in all gnammas on all rocks (Figures 4–9). *Parabornella tounoiri* were fourth instars that had been in suspended animation (Jones 1971). Following reactivation they soon pupated and adults emerged and dispersed, so larval numbers dropped rapidly. This pattern was very different to that of *Chironomus tepperi* which colonised some ponds from

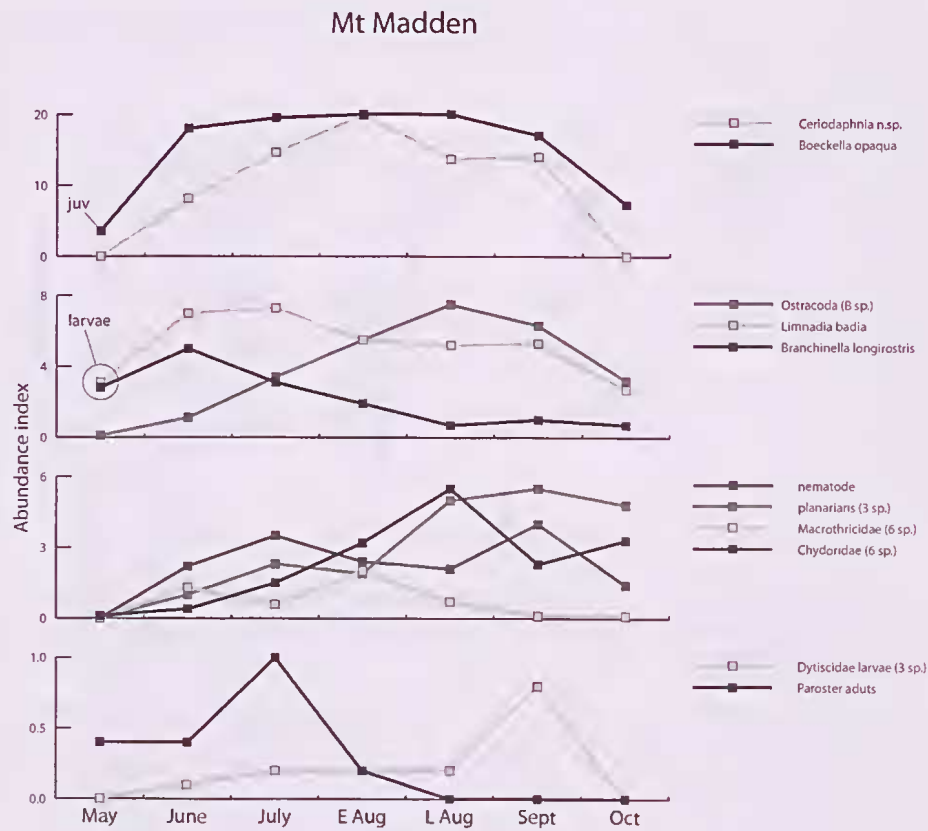


Figure 4. Seasonal changes in 11 taxa/taxonomic groups on Mt Madden. Abundance indices in Figures 4–9 are calculated by adding all abundance values for all pools, and hence show the relative success of a taxon on a rock, as measured by its pooled abundances in the 10 study gnammas. Circles on the figures indicate abundances were due to larvae.

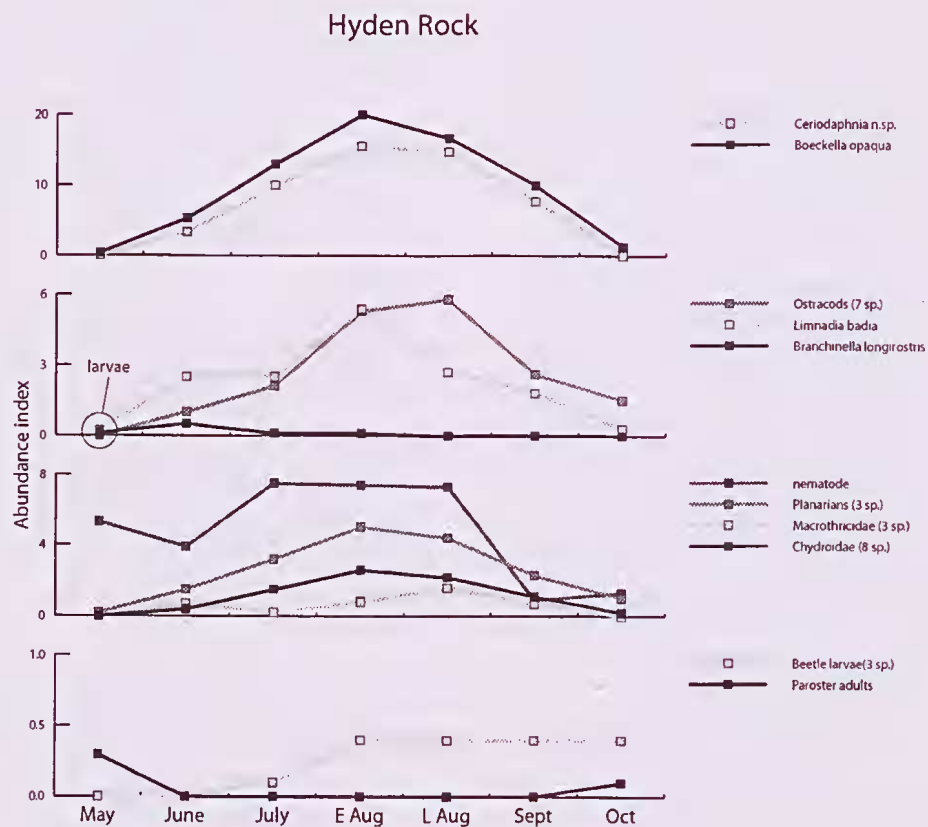


Figure 5. Seasonal changes in the same 11 taxa/taxonomic groups in the same order on Hyden Rock

Yanneymoon Rock

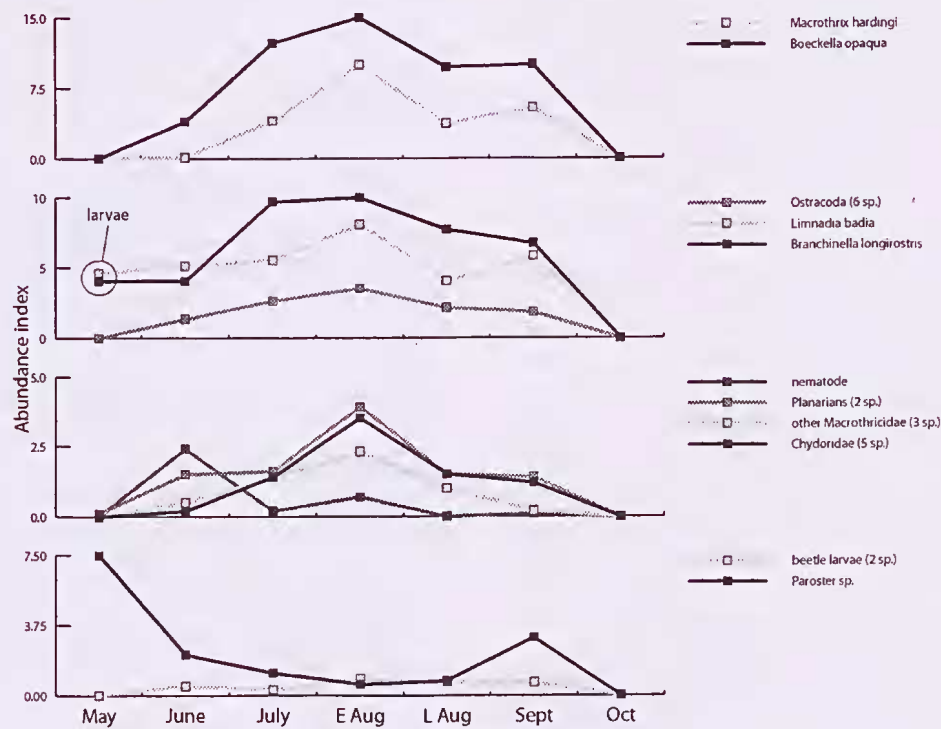


Figure 6. Seasonal changes in the same 11 taxa/taxonomic groups (with *Macrothrix hardingi* substituted for *Ceriodaphnia n. sp.*) in the same order on Yanneymoon Rock.

Bullamany Rock

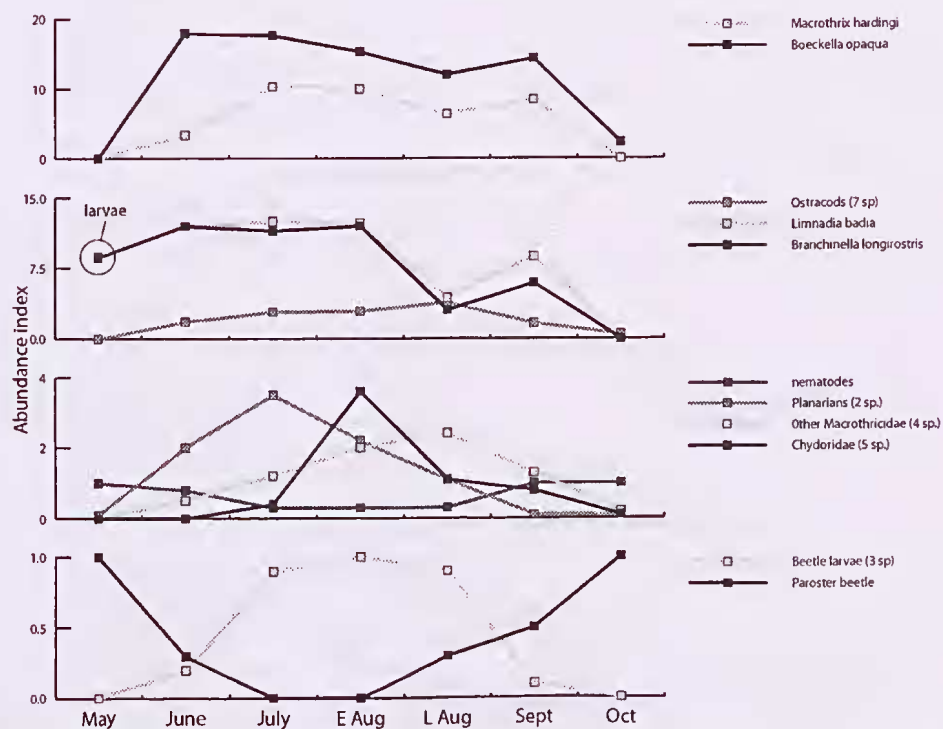


Figure 7. Seasonal changes in the same 11 taxa/taxonomic groups (as on Yanneymoon Rock) in the same order on Bullamany Rock.

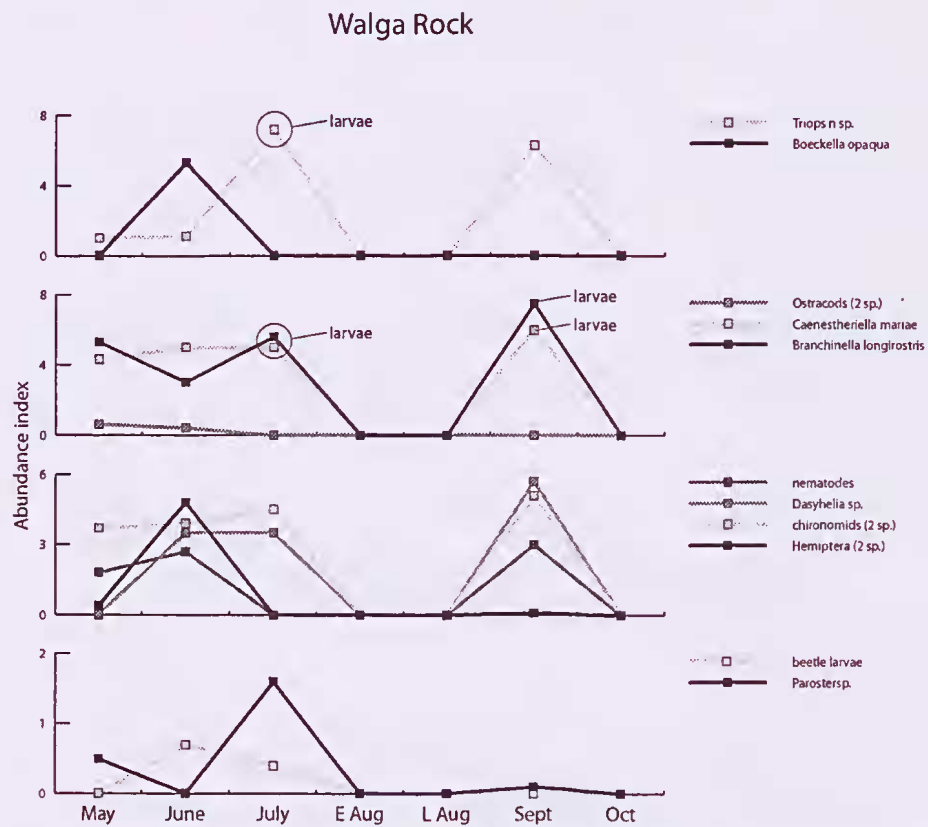


Figure 8. Seasonal changes in 11 common taxa/taxonomic groups on Walga Rock (these are not comparable with those on the other four rocks).

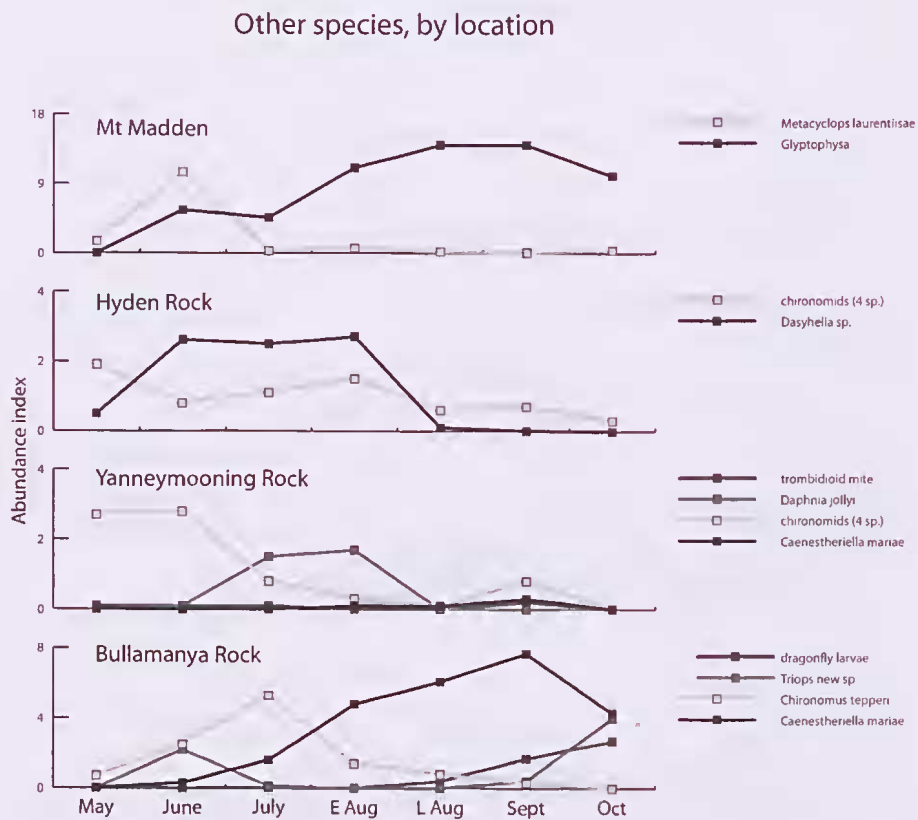


Figure 9. Seasonal changes in some other common species that are largely restricted to, or most common on, particular rocks.

semipermanent waters nearby (as at Bullamany Rock) so that its numbers peaked in week 6 (Figure 9). Another early starter in Mt Madden was the cyclopoid *Metacyclops laurentiisae* which appeared early on as adults and then increased rapidly by the next visit in June before falling to low numbers through the remainder of the hydroperiod (Figure 9). The branchiopods, *Branchinella longirostris* and *Limnadia badia* matured early and were most common over the next 3–9 weeks, waning in the last 6–9 weeks (Figures 4–7), though *L. badia* often persisted until pools dried. *Triops* n. sp. was also a quick developer and hatched repeatedly if the pools dried and re-wetted (as at Walga and Bullamany Rocks) (Figures 8, 9). They occurred almost exclusively in pools with flat rocks and usually were found hiding under these rocks. On the other hand the clam shrimp *Caenestheriella mariae* developed somewhat slower reaching a peak in the middle or late life of pools (Figures 8, 9). All of the branchiopods were univoltine.

Less prominent early starters were the planarians (Figures 4–7) peaking 6–12 weeks after filling, with the black planarian developing quicker than the green species and waning earlier; it was also the most widespread planarian while the rhabdocoel was restricted in distribution to the south and limited in abundance. Nematodes were most common in southern rock pools and peaked variously at 6–18 weeks (Figures 4–8).

Some insects invaded the southern rocks early on; the most prominent of these was the beetle *Paroster*, particularly on Yanneymooning where it peaked very early and again as pools dried (Figures 4–8). Larvae appeared 3–6 weeks into the hydroperiod and were small but by 12–15 weeks were relatively large and in declining numbers as the pools dried at 15–18 weeks. Other beetles, mainly *Sternopriscus multimaculatus* and *Eretes australis*,

also successfully bred in many of the pools, mainly in the south. An insect which failed to breed successfully in the short hydroperiod of 2010 was the odonatan *Hemicordulia tau*. On Bullamany (Figure 9), large numbers of immature larvae died in early October in some pools, while elsewhere only a few immature individuals died; in all cases there was no evidence that any matured and emerged. Of the few hemipterans visiting the pools, *Micronecta* sp. was the most common followed by *Auisops thienemannii*. Most hemipterans bred, and while some matured before the pools dried prematurely, many did not in 2010.

Boeckella opaquia, the most common invertebrate of most pools, variously peaked at 3–9 weeks (Figures 4–8). It had a few overlapping generations, and hence was multivoltine. The other abundant open-water plankters included *Ceriodaphnia* n. sp., *Macrothrix hardingi* and occasionally *Daphnia jollyi*, which all tended to peak in the 12th week (Figures 4–9), i.e. after the open-water branchiopods, and all three were multivoltine with overlapping generations. There were many benthic cladocerans peaking at various times with little overall pattern, though the majority of the abundant ones also peaked in the 12th week (Figures 4–7). Again the presence of numerous juveniles of most species during the season suggest most are multivoltine. All had ephippial eggs as the pools shrunk and dried. Ostracods tended to peak a little later than cladocerans, in the 12–15th weeks (Figures 4–7). It was not uncommon for them to persist longer than other crustaceans and dried remains in pools often featured shells of *Ilyodromus* and *Beunelongia*, as well as those of *Limnadia badia*. Once mature, the larger ostracods such as *Beunelongia*, *Cypretta* and *Ilyodromus* did not vary in size so were probably univoltine. No data were collected on the smaller taxa such as *Cypricercus*.

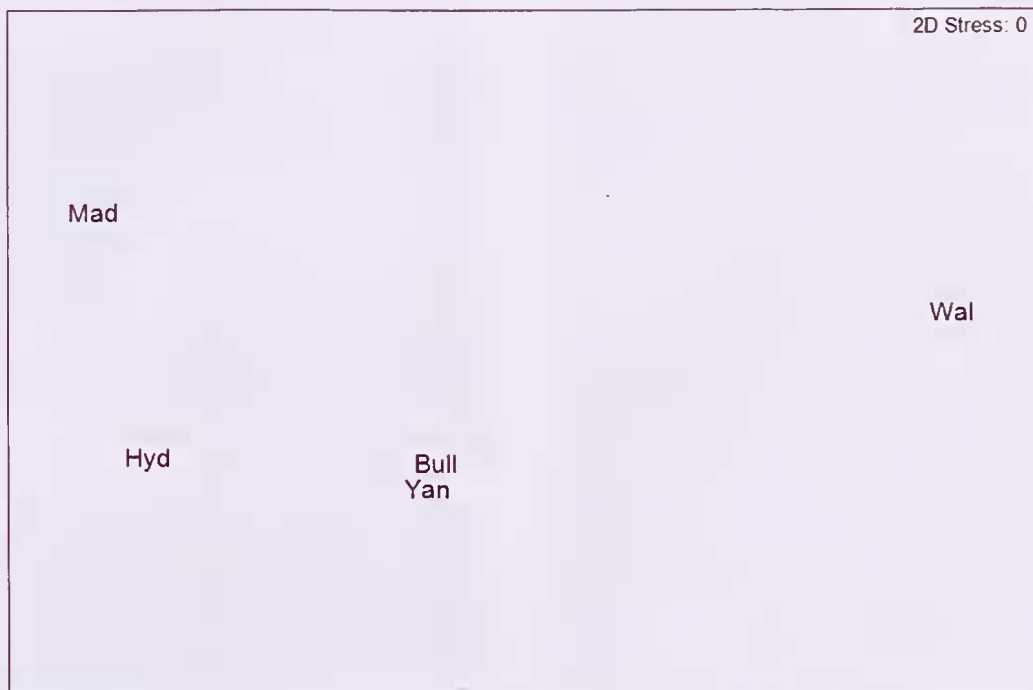


Figure 10. Ordination diagram of the relative dissimilarity of the invertebrate assemblages on the five rocks.

Few dipteran larvae were recorded except for some chironomids. Mosquitoes were particularly uncommon as were various larvae such as stratiomyids and tabanids. Ceratopogonids were common in some pools on some rocks; those in Mt Madden and Yanneymooring peaked late (12–15 weeks), while those on Hyden Rock peaked early (3–9 weeks) then suddenly waned.

Only Mt Madden had the snail *Glyptophysa*. It appeared early as adults, bred and then numbers peaked at 9–12 weeks (Figure 9). As the pools dried, populations disappeared to under rocks on mud where adults and maturing juveniles began aestivating. At this stage they were easily activated again by immersing in water. Numbers under rocks did not match the large numbers seen in pools during the height of the season.

Few mites were recorded but included terrestrial trombidoid mites. These persisted for a few weeks after filling in Yanneymooring and Bullamany Rocks and at Yanneymooring they were back again as the pools dried (Figure 9). During the dry season, at least in the October visit and on an extra November visit to Yanneymooring, they could be found under rocks and amongst coarse gravel.

DISCUSSION

Species richness and composition amongst temporary pools, even within sites is highly variable (Pinder *et al.* 2000; Jocqué *et al.* 2007b) so that authors prefer to make species lists for districts or whole rocks rather than for individual or small groups of pools (Bayly 1982, 1997; Pinder *et al.* 2000; Jocqué *et al.* 2007a). Considering district totals, the 72 species recorded from this study compares with 88 species from just 36 gnammas on 17 different granite outcrops across the wheatbelt (Bayly 1997). The more wide ranging and detailed study of Pinder *et al.* (2000) recorded 230 species across a much wider area of southwestern Western Australia (but only from nine rocks and an unspecified number of pools). Clearly, district cumulative species richness (CSR) depends on the size of the district so that it is more instructive to consider CSR on individual outcrops. For the Western Australian Wheatbelt CSR per rock outcrop is around 45–60 species; Pinder *et al.* (2000) quoted 49 ± 15 in their study, Jocqué *et al.* (2007a) listed 58 taxa for Hyden (Wave) Rock and 43 taxa for King Rocks, and the present study recorded 47 species on Hyden Rock, and between 22 and 54 species for the other four rocks. These figures well exceed the <20 CSR for rockpools in other parts of the world (Jocqué *et al.* 2010) and in eastern Australia (Bishop 1974; B V Timms unpubl. data). The number of species per pool during the period of maximum diversity is around 25–30 (except on Walga Rock), which is higher than figures given by other authors: for example Bayly (1997) listed 7–15 species for pools on Mt Madden. Discrepancies could be due to different sampling techniques, sampling at different stages in the hydrologic cycle and taxonomic expertise. Also there could be differences between years, though the data from the study rocks (Table 1) suggests a similar composition in 2009 and 2010 except for numerous uncommon species encountered in 2010 with greater sampling effort. The significantly lower diversity in the north clearly was associated with its shorter and unreliable hydroperiods on the phenology of some

species, as experienced during 2010 on Walga Rock (Vanschoenwinkel *et al.* 2009, 2010). The same factor operated to a much lesser degree on the next rock to the south, Bullamany, where at least *Hemicodulia tau* failed to complete its life cycle in 2010.

Despite the high variability in species richness and species composition on and between rocks, it seems there may be a pattern across the southwest of Western Australia. Compared to gnammas in the central Wheatbelt, the pools in the forested west and southwest corner of Western Australia studied by Bayly (1982) have a reduced fauna of 35 species overall, with fewer species in most groups, particularly turbellarians and beetles. Similarly gnammas well north of the Wheatbelt, such as Walga Rock have fewer species, again in most groups, but most noticeably among cladocerans, tubellarians and beetles. In both cases dominants are largely similar to those in the central Wheatbelt. There is also a decrease in species richness from south to north as seen in the present study and the more detailed assessment by Jocqué (2007) and Jocqué *et al.* (unpubl. data). These differences, and maybe there are also changes east to west (B V Timms unpubl. data), must be associated with major climatic differences though habitat parameters may also be influential (Vanschoenwinkel *et al.* 2009). Central is the reliability of rainfall and lengths of hydroperiod, as well as perhaps temperature and evaporation potential differences, between the central Wheatbelt and fringe areas. Rainfall gradients are from the southwest to the northeast, so not quite concordant with the axis of the study rocks, whereas temperature gradient and evaporation potential are more south–north oriented. There could also be a difference in food sources. Bayly (1982) mentioned the importance of organic matter input from decaying mosses and lichens in the Northcliffe pools and recorded few plants in these pools. By contrast in central Wheatbelt gnammas, organic matter derived from mosses and lichens does not seem so important, and the influence of vegetation, particularly of *Isoetes* and *Glossostigma*, stronger on features such as habitat complexity and possibly on periphyton availability. Northern sites such as Walga Rock lack vegetation (and hence the microcrustaceans associated with this habitat) and as seen in 2010 can have reduced hydroperiods preventing completion of life cycles.

Salinity is an important environmental control in many Australian waters (Pinder *et al.* 2002 for southwestern Australia) and in some temporary waters (Waterkeyn *et al.* 2008), but not in gnammas. The study gnammas contained waters of low to very low total dissolved salts and they remained fresh throughout the hydroperiod. Salinity thresholds for Australian inland aquatic fauna are higher by at least an order of magnitude (Hart *et al.* 1991), so this factor was dismissed as inapplicable in this study.

Habitat structure is important for the presence of some species. On both Bullamany and Walga Rocks, *Triops* n. sp. occurred only in pools with flat rocks standing off the bottom, probably as such arrangements provided refuges against predation from birds in pools with crystal-clear water. The snail *Glyptophysa* survived only in those pools with large rocks on Mt Madden (and also Anderson Rocks and King Rocks: B V Timms unpubl. data) probably because the protected undersides of such rocks

provide aestivation refuges. Chironomids and ceratopogonids were most common in pools with thicker organic sediments which may provide the most suitable habitat and food, but this was not investigated quantitatively.

As recorded in other studies (Bayly 1982, 1997; Pinder *et al.* 2000), regional endemism is high, mainly among the crustaceans which tend to have lower dispersability. The list includes many of the dominants such as *Branchinella longirostris*, *Limnadia badia*, *Pleurispina* spp. *Ceriodaphnia* n. sp., *Daphnia jollyi*, *Macrothrix hardingi*, *Bennelongia* sp 563, *Boeckella opaquia* and *Allotrissocladius* sp 1 (an insect). An addition to the list of endemic species is the new subspecies of *Triops* which lives in northern gnammas in this study but is found rarely in gnammas in the Hyden area (B Vanschoenwinkel pers.comm. 2011).

The high diversity and endemism of invertebrates in gnammas in the wheatbelt is typical of inland waters of southwestern Australia and applies to many invertebrate groups [e.g. *Branchinella* (Timms 2002, 2008); *Coxiella* (Pinder *et al.* 2002); chydorid cladocerans (R. Shiel pers.comm. 2008); *Daphnia* (*Daphniopsis*) (Hebert & Wilson 2000); mytilocyprinid and other ostracods (Halse & McRae 2004; Pinder *et al.* 2002); and *Parartemia* (Timms 2010)]. Diversity and endemism is believed to be promoted by past climate change and the role of isolated refugia, isolated granitic outcrops with their stressful but reliably filled seasonal pools being particularly ideal locations for speciation (Hopper *et al.* 1997).

Jocqué *et al.* (2007a) mentioned two basic classes of inhabitants in these gnammas, passive and active dispersers, while Williams (1985) based on Wiggins *et al.* 1980 recognised a more detailed classification of four types (I to IV). All the crustaceans (large and small branchiopods, copepods, cladocerans, ostracods), planarians and the snail *Glyptophysa* sp. belong to Wiggins *et al.*'s Group I [type (a) of Williams], the permanent residents capable of only passive dispersal. Almost all of these survive the desiccated period as resistant eggs, but the cyclopoid copepod *Mesocyclops laurentisae* seems to pass the summer in some advanced copepodite stage (as do some overseas cyclopoids in winter: Smyly 1958), and the snail as quiescent adults. A few species belong to Wiggins *et al.*'s Group II [type (b) of Williams] which includes the residents capable of some active dispersal. Examples are some of the chironomids, including *Parabornella tonnoiri*. These survive the dry summer as cryptobiotic 4th instars and the adults are capable of limited airborne dispersal during the wetted period (Jones 1971; Edwards 1968). The remainder belong to Group IV [type (c) of Williams]; they are all insects (hemipterans, coleopterans, various dipterans including some chironomids such as *Chironomus tepperi* living in the pools when wet, but surviving elsewhere during the dry period. Wiggins *et al.*'s type III does not need water for breeding; the only example in the present pools is the terrestrial trombidoid mites, which are really accidental members of the aquatic fauna of these pools. Williams (1985) dismissed this group and erected another type (d) that are found only in temporary waters moving from one to the next as they fill and dry over the year. There are no members of this group in these pools as generally all are wet in winter-spring and dry over summer-autumn.

The generalists [Group IV and type (c)] live in many types of habitats (Jocqué *et al.* 2007a). A prime example is the Coleoptera with many of the species recorded in gnammas widespread and found living in a variety of waters including swamps, marshes and freshwater and saline lakes (Pinder *et al.* 2000). Hendrich & Frey (2008) mentioned eight visiting species (to four granite outcrops), Pinder *et al.* (2000, 2002) 23 taxa (to nine granite outcrops), and the present study 16 species (to five granite outcrops), making 28 species altogether. This is the first study to find so many species breeding, with eight different type of larvae recorded. An exception to more generalists beetles appears to be *Paroster* which has some species focusing on pan gnammas, visiting them early in their existence to breed and during the wet phase utilising them to the exclusion of other pools in the area (B V Timms unpubl. data). Hendrich & Frey (2008) surmised that at least *P. baylyi* and *P. ursulae* may pass the summer as resistant eggs in pan sediments just like the crustaceans. This study suggests this is unlikely, as *Paroster* near *michaelseni* oversummers elsewhere, arrives to breed when the pans first fill, larvae grow in the pans during their wet phase (small in weeks 3–12, larger in weeks 12–18) and mature before the pans dry, giving a second peak of adults. They behave ecologically like the majority of insects and not like the crustaceans, and their life cycle is adapted to the hydrological regime of pan gnammas. The same does not apply to some of the other generalists found in gnammas, for instance odonates and many hemipterans did not complete their life cycle in 2010. Though this study did not focus on dispersal, the greater dispersal ability of the generalist insects *vis-à-vis* the passive crustaceans, is revealed by their appearing in more pools per rock than similarly classified uncommon crustaceans (cf. Tables 1 and 2).

Succession in these pools is explained largely by the tolerance model of Connell & Slatyer (1977) with perhaps some aspects of their inhibition model applying. In most pools the habitat changed little during the wetted period: plants quickly appeared in most pools but did not dominate the water column; salinity increased a little, but still well within tolerance limits; most pools had crystal-clear water throughout their existence. So successional stages associated with vast habitat changes as seen in the Pomboineit pool (in Victoria) studied by Lake *et al.* (1989) would not be expected. Neither were there major changes in predation pressure as seen in that study – the major predators, planarians and beetle larvae, were generally abundant throughout weeks 6–15 with certainly no obvious peak towards the end as in the Pomboineit study (Lake *et al.* 1989). It is possible that this pressure eliminated fairy shrimps in many pools and cladocerans then dominated, as predicted by Jocqué *et al.* (2007b). However, this study was too coarse to be sure of this and, besides, the averaging method of recording abundance and species richness in the pool sets blurred changes in individual pools. It would seem that most species in these pools developed largely independently of others, reaching their peak numbers and endurance according to their phenological characteristics, i.e. pool dynamics fall largely within the scope of the tolerance model of succession. The unusually short hydroperiod of 2010 was long enough for all the passive dispersers [Types I and II, (a) and (b)] to complete their life cycle, but not for some of the generalists [Types IV and (c)].

Presumably during a 'normal' year when hydroperiods extend to October and November all generalists complete their life cycle, but composition of invertebrate assemblages at such times is unknown. Based on 2010 data, it is predicted many pools would be dominated by *Limnadia badia*, *Boeckella opaquia* and various ostracods.

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Appendix 1 Seasonal changes in abundance indices for selected species at the five sites.

Mt Madden	24 May	17 Jun	10 Jul	1 Aug	24 Aug	12 Sep	3 Oct
Planarians (3 spp.)	-	1.0	2.3	1.9	6.0	5.6	4.8
Nematode	-	2.2	3.5	2.4	2.1	4.0	1.4
Branchiopod larvae	5.9	-	-	-	-	-	-
<i>Branchinella longirostris</i>	-	5.0	3.1	1.9	0.7	1.0	0.7
<i>Limnadia badia</i>	-	7.0	7.3	5.5	5.2	5.3	2.7
<i>Boeckella opaquua</i>	3.6j	19.0	20.5	20.3	21.7	17	7.3
<i>Metacyclops laurentiisae</i>	1.5a	10.5	0.3	0.6	0.2	0.1	0.4
Harpacticoid sp 674	-	1.0	0.4	-	-	-	-
<i>Ceriodaphnia n.sp.</i>	-	8.1	14.6	19.9	13.7	14.0	-
<i>Moina australiensis</i>	-	1.6	1.3	-	1.3	1.7	-
<i>Macrothrix hardingi</i>	3.6	-	-	-	-	-	-
Macrothricidae (6 spp.)	-	1.3	0.6	2.0	0.7	0.1	0.1
Chydoridae (6 spp.)	0.1	0.4	1.5	3.2	5.5	2.3	3.3
Ostracoda (8 spp.)	0.1	1.1	3.4	5.5	8.3	6.3	3.2
Odonata larvae	-	-	-	-	-	0.4	0.1
Hemiptera (4 spp.)	0.2	0.3	0.1	0.2	0.2	0.3	0.1
<i>Paroster</i> adults	0.4	0.4	1.0	0.2	-	-	-
Other Coleoptera (6 spp.)	0.1	0.1	0.1	0.4	0.3	0.2	-
Dytiscidae larvae (3 spp.)	-	0.1	0.2	0.2	0.2	0.8	-
chironomids (3 spp.)	-	0.1	1.2	1.2	0.4	0.9	-
<i>Dasyhelius</i> sp.	-	-	-	-	0.1	-	1.8
<i>Aedes alboannulatus</i>	-	-	-	0.1	-	-	-
<i>Glyptophysa</i>	-	5.6	4.6	11.0	14.0	14.0	10.0

J, juveniles; a, adults

Hyden Rock	24 May	17 Jun	12 Jul	1 Aug	24 Aug	12 Sep	4 Oct
Planarians (3 spp.)	0.2	1.5	3.2	5.0	4.4	2.3	1.0
Nematode	5.3	3.9	10.1	9.7	9.3	0.9	1.3
Branchiopod larvae	0.1	-	-	-	-	-	-
<i>Branchinella longirostris</i>	-	0.5	0.1	0.1	-	-	-
<i>Limnadia badia</i>	-	2.5	2.5	5.4	2.7	1.8	0.3
<i>Boeckella opaquua</i>	0.3	5.3	13.0	20.0	16.7	10.0	1.3
<i>Ceriodaphnia n.sp.</i>	-	3.3	10.0	15.6	14.7	7.7	-
<i>Moina australiensis</i>	-	-	0.1	-	0.1	1.7	1.3
Other Macrothricidae (3 spp.)	-	0.7	0.2	0.8	1.6	0.7	-
Chydroidae (8 spp.)	-	0.4	1.5	2.6	2.2	1.1	0.2
Ostracods (7 spp.)	-	1.0	2.1	5.3	5.8	2.6	1.5
Hemiptera (4 spp.)	-	0.3	-	0.1	0.3	0.5	0.4
<i>Paroster</i> adults	0.3	-	-	-	-	0.1	-
Other beetle adults (8 spp.)	0.1	0.1	0.1	0.2	0.1	0.1	-
Beetle larvae (3 spp.)	-	-	0.1	0.4	0.4	0.4	0.4
Chironomids (4 spp.)	1.9	0.8	1.1	1.5	0.6	0.7	0.3
<i>Dasyhelius</i> sp.	0.5	2.6	2.5	2.7	0.1	-	-
<i>Aedes alboannulatus</i>	-	-	2.5	-	0.3	-	-

Yanneymoon Rock	25 May	18 Jun	11 Jul	2 Aug	25 Aug	13 Sep	5 Oct ¹
Planarians (2 spp.)	0.1	1.5	1.6	3.9	1.5	1.4	-
Nematode	-	2.4	0.2	0.7	-	0.1	-
Branchiopod larvae	4.3	-	-	-	2.7	3.7	-
<i>Branchinella longirostris</i>	2.0j	4.0j	9.7	10.3	7.7	6.7	-
<i>Limnadia badia</i>	2.3j	5.1	5.5	8.1	4.0	5.8	-
<i>Caenestheriella mariae</i>	-	-	-	0.1	0.1	0.3	-
<i>Boeckella opaquua</i>	-	3.9	12.3	15.3	9.7	10.0	-
<i>Ceriodaphnia n.sp.</i>	-	0.2	-	-	-	-	-
<i>Daphnia jollyi</i>	-	0.1	1.5	1.7	-	-	-
<i>Macrothrix hardingi</i>	-	0.1	4.0	10.0	3.7	5.4	-

Yanneymoon Rock (cont.)	25 May	18 Jun	11 Jul	2 Aug	25 Aug	13 Sep	5 Oct ¹
Other Macrothricidae (3 spp.)	-	0.5	1.4	2.3	1.0	0.2	-
Chydoridae (5 spp.)	-	0.2	1.4	3.5	1.5	1.2	-
Ostracoda (6 spp.)	-	1.3	2.6	3.5	2.1	1.8	-
Hemiptera (4 spp.)	-	0.1	0.6	0.1	0.6	0.8	-
Odonata	-	-	0.3	-	-	0.2	-
<i>Paroster</i> sp.	7.5	2.2	1.2	0.6	0.8	3.1	-
other beetles (2 spp.)	0.1	0.3	0.7	0.3	0.4	0.2	-
beetle larvae (2 spp.)	-	0.5	0.3	0.9	0.7	0.7	-
chironomids (4 spp.)	2.7	2.8	0.8	0.3	0.1	0.8	-
<i>Dasyhelius</i> sp.	-	-	0.1	-	0.4	2.0	-
<i>Aedes alboannulatus</i>	-	0.5	1.0	0.4	-	-	-
Trombidoid mite	0.1	0.1	0.1	-	-	0.2	-

¹ Dry

j, juveniles

Bullamany Rock	26 May	19 Jun	12 Jul	3 Aug	26 Aug	14 Sep	5 Oct
Planarians (2 sp.)	0.1	2.0	3.5	2.2	1.1	0.1	0.1
Nematodes	1	0.8	0.3	0.3	0.3	1.3	1.3
Branchiopod larvae	17.2	-	-	-	3.7	-	-
<i>Branchinella longirostris</i>	-	12	11.5	12.0	3.0	5.9	-
<i>Limnadia badia</i>	0.1	12	12.5	12.3	4.3	8.7	-
<i>Caenestheriella mariae</i>	-	1.6	6.1	7.7	4.3	2.8	0.3
<i>Triops</i> n. sp.	-	2.2	0.1	-	-	0.4	4.0
<i>Boeckella opaquia</i>	-	17.9	17.6	15.3	12.0	14.3	2.3
<i>Daphnia jollyi</i>	-	-	0.1	1.7	-	-	-
<i>Moina australiensis</i>	-	-	-	-	-	0.3	1.3
<i>Macrothrix hardingi</i>	-	3.3	10.3	10	6.3	8.4	-
Other Macrothricidae (4 spp.)	-	0.5	1.2	2.0	2.4	1.3	0.2
Chydoridae (5 spp.)	-	-	0.4	3.6	1.1	0.8	0.1
Ostracods (7 spp.)	-	1.8	2.8	2.9	3.8	1.6	0.5
<i>Anisops gratus</i>	-	0.5	-	-	-	0.2	0.1
Dragonfly larvae	-	-	-	-	0.4	1.7	2.7
<i>Paroster</i> beetle	1.7	0.3	-	-	0.3	0.5	1.0
Other beetle adults (5 spp)	-	0.1	0.1	0.1	0.3	0.2	0.1
Beetle larvae (3 spp.)	-	0.2	0.9	1.0	0.9	0.1	-
<i>Chironomus tepperi</i>	0.7	2.5	5.3	1.4	0.8	0.3	-
Other chironomids (5 spp.)	0.3	1.4	3.2	1.3	1.4	0.8	-
<i>Aedes alboannulatus</i>	2.0	1.0	0.5	-	-	-	-
<i>Dasyhelius</i> sp.	-	-	0.5	3.3	5.0	-	-
Trombidoid mites	0.1	0.1	0.1	-	-	-	-

Walga Rock	27 May	20 Jun	15 Jul	4 Aug ¹	14 Sep	6 Oct ¹
Nematodes	1.8	2.7	-	-	3.0	-
Branchiopod larvae	4.0	-	17.2	-	16.8	-
<i>Branchinella longirostris</i>	5.3	3.0	-	-	-	-
<i>Caenestheriella mariae</i>	4.3	5.0	-	-	-	-
<i>Triops</i> n. sp.	1.0	1.1	-	-	6.3	-
<i>Boeckella opaquia</i>	-	5.3	-	-	-	-
Ostracods (2 spp.)	0.6	0.4	-	-	-	-
Hemiptera (2 spp.)	0.4	4.8	-	-	0.1	-
<i>Paroster</i> sp.	-	-	1.6	-	-	-
Other beetles (4 spp.)	-	0.1	0.6	-	0.5	-
Beetle larvae	-	0.7	0.4	-	-	-
Chironomids (2 spp.)	3.7	3.9	4.5	-	5.1	-
<i>Dasyhelius</i> sp.	-	3.5	3.5	-	5.7	-

¹ Dry